Rev. Écol. Biol. Sol, 1988, **25** (4) : 373-384.

Trèe root and macrofauna effects on nitrification and mineral nitrogen losses from deciduous leaf litter

BY

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Synopsis: Experimental chambers containing oak leaf litter were established in the field with and without living tree roots. Negligible nitrate losses occurred from root treatments although millipedes enhanced ammonification. When the roots connected to animal treatments were cut nitrate losses increased 11 fold after 7 days suggesting that nitrate uptake by roots accounted for the apparent inhibition of nitrification.

Keywords: Nitrogen mineralisation, millipedes, nitrification, tree roots, leaf litter, deciduous forest.

INTRODUCTION

The processes of nitrification are well documented in terms of microbial physiology (VERSTRAETE, 1981) but less is known about the controls over *in situ* rates of nitrification in forest soils. Site factors such as moisture, temperature, pH and soil C/N ratios have been found to explain little of the variance in laboratory determinations of relative nitrification (the proportion of nitrate-N in net N mineralisation) (ROBERTSON, 1982) though there are still conflicting views on allelopathic suppression of nitrification (BALDWIN *et al.*, 1983; SIVAPALAN & FERNANDO, 1985; MCCARTY & BREMNER, 1986). However, in acid forest soils where rates of N-mineralisation are low a key factor appears to be the efficiency of roots in reducing ammonium availability to nitrifiers (COOPER, 1986; RIHA *et al.*, 1986). Under these conditions populations of autotrophic nitrifiers are low and their response time to increased ammonium availability is also reduced in acid soils

Reçu le 31-07-88.
Accepté le 12-01-89.

(SARATHCHANDRA, 1978; VERSTRAETE, 1981) resulting in a lag, sometimes of considerable duration, before the onset of nitrification (VITOUSEK *et al.*, 1982; VITOUSEK & MATSON, 1985).

We have shown that macrofauna (millipedes, woodlice, earthworms, etc.) alter the timing and magnitude of ammonification in litter and humus in relation to microbial processes alone (ANDERSON *et al.*, 1985 *a*, 1985 *b*; ANDERSON & INESON, 1983, 1984). Animals also enhance nitrification or accelerate the onset of nitrification in laboratory incubations (ANDERSON *et al.*, 1985 *b*). The presence or absence of a root sink will clearly affect the dynamics of these systems and hence we investigated the use of small chambers with implanted tree roots in an oak woodland (ANDERSON *et al.*, 1985 *a*). In these experiments negligible nitrification occurred in litter over a period of 6 weeks in the field although millipedes (*Glomeris marginata*) doubled N-mineralisation rates as ammonium.

The present experiment was set up to investigate the effects on nitrification processes of increased ammonium availability over a period of several months in the field and the effects of cutting roots on nitrification. Aged oak leaf litter was used as experimental material to avoid the complications of rapid initial changes in polyphenol concentrations in fresh litter and their potential allelopathic effects.

I. — METHODS

A) Site

The Perridge field site (NGR SX 925961) is a stand of 50-60 year old oak trees (*Quercus robur*) with a thin understory of young beech trees (*Fagus sylvatica*). The soil is typical of deciduous woodlands growing on low base-status parent material (Culm Measure shale) in S. W. England in having a compact, highly organic humus layer (80% ignition losses, 30 to 70 mm in depth with a moder humus form, *sensu* KUBIENA, 1953) and a mean soil pH in the range 3.7 to 4.5. Mean annual soil temperatures at 50 mm depth are around 10.5°C and mean annual precipitation for the area is 850 mm. Oak and beech leaf litter is fragmented in about 18 months so that surface litter is present throughout the year.

B) Experimental chambers

Details of the experimental chambers are given in ANDERSON & INESON (1982). These consist of a perspex chamber, approximately 7 cm in diameter, with a sloping base and a drainage port for leachates. The bottom of the chamber is covered by a bed of polyethylene beads (Alkathene, Imperial Chemical Industries) supporting an inner chamber, with a fine-mesh base, holding the experimental materials. The chambers are closed with a lid which has a central access hole. This was plugged with cotton wool in the present experiments to allow gas exchange but reduce moisture losses.

Living roots were introduced into half of the set of experimental chambers at the start of the experiment. An intact length of fine root, bearing healthy ectomycorrhizal tips, was teased from the interface of the litter and humus layers and carefully introduced through a slit cut down the side of the chamber and bedded down in some humus material on a mesh disc covering the drainage bed. The inner chambers containing F-layer material were placed on top and silicone grease was used to seal the slit and the area around the root entry to the chamber.

Leachate sampling was carried out by attaching a wash bottle containing 60 ml distilled water to the drainage port of each chamber, irrigating the system twice with water and then sucking out all the free-draining water. The leachates were then returned to the laboratory for analysis.

C) Experimental materials and treatments

Litter (F-layer) material was collected from the site in February 1984. The leaves were air dried, lightly crushed after removing mid-ribs and then sieved to prepare a 5 to 20 mm fraction. Aliquots of material, equivalent to 2.09 g oven dry wt leaves, were placed in the inner containers, rewetted with distilled water and inoculated with a suspension of fresh leaf litter. Samples of well-leached, H-layer material (0.94 g oven dry wt) were prepared for packing roots and adding to all other treatments as outlined above.

Eighteen chambers, twelve with living root implants, were set up on 20 March 1984 and left for four weeks. At the end of that period the roots appeared healthy and showed new growth. Millipedes (two *Glomeris marginata* with a total fresh weight of 200 mg) were introduced into previously designated chambers. Thus the following treatments, each with three replicates, were established on 17 April:

- without animals, without roots ($-A-R$),
- with animals, without roots ($+A-R$),
- without animals, with roots ($-A+R$),
- with animals, with roots ($+A+R$),
- without animals, with roots (to cut) ($-A+R_c$),
- with animals, with roots (to cut) ($+A+R_c$).

Leaching was carried out every 7 days for 12 weeks until 14 July when the roots in the designated treatments (R_c) were cut where they entered the experimental chamber. At this time some of the millipede treatments ($+A$) were found to contain insufficient litter for the second phase of the experiment and aliquots of the same experimental litter (equivalent to 0.95 g oven dry material) were added to treatments. The systems were monitored for a further 12 weeks until 13 October 1984 when the experiment was terminated.

Integrated mean soil temperatures, at 5 cm depth below the litter layer, were determined weekly using Zeolite capsules (T. A. Cells, Woden, Australia). The capsules take up water according to a $Q_{10}=2$ temperature response and hence integrated temperatures over time intervals are a funtion of mass increments.

D) Leachate and litter analysis

Leachates were stored at 5°C until analysis was complete; normally within a few days of sampling. Measurements of pH were made on leachates before analysis for mineral-N concentrations using a Bemas Autoanalyser (Burkard Instruments, U.K.). Ammonium-N and nitrate-N were determined by the alkaline phenate/sodium nitroprusside and sulphanilamide/copper hydrazine methods respectively.

Total nitrogen content of the leaf litter was determined by Kjeldahl.

Total polyphenols in freshly fallen litter (November 1983) and in the experimental litter were determined using the Folin-Denis method (ALLEN *et al.*, 1974) and calibrated against tannic acid standards to express the results as mg g^{-1} oven dry wt leaf material.

E) Data analysis

Results of leachate analysis are expressed as μg element released per chamber. Data for pH were detransformed to H^+ concentration before analysis. Arcsin transformation was used for the comparison of the proportion of nitrate-N/total mineral-N in leachates to investigate whether roots take up nitrate-N preferentially. Treatments were compared by analysis of variance of total mineral-N losses over weeks 1-12 or 13-25 from each chamber. As a consequence of damage to some experimental units (*see* below) two replicates per treatment were used for analysis so that balanced, two-way (animals/roots) and three-way (animals/roots/time) anovas of mineral-N and H^+ could be carried out. One-way anova

was used to test differences between treatment at the end of the 12 week or 25 week periods and the $+A+R_c$ treatments before and after cutting the roots.

II. — RESULTS

A) Analysis of experimental litter

The nitrogen content of the experimental F-layer litter collected in February was 1.5% compared with 1.1% in freshly fallen leaves in November.

Total polyphenol concentration (mean ± 1 SE) were 86.0 ± 1.7 mg g^{-1} for freshly fallen material and 3.7 ± 0.2 mg g^{-1} for the experimental litter. The results for nitrogen and polyphenol analysis confirm that the F-layer material used in these experiments was in a well leached and decomposed condition.

B) Soil temperature

Integrated-mean soil temperatures are shown in Figure 1 A. Temperatures increased from 8 to 15°C during the first 4 weeks of the experiment, fell to around 10°C for the next 5 weeks and then remained between 13 and 16°C for all but the last two weeks of the experiment. The arithmetic mean of weekly temperature values for the duration of the experiment was 12.6°C.

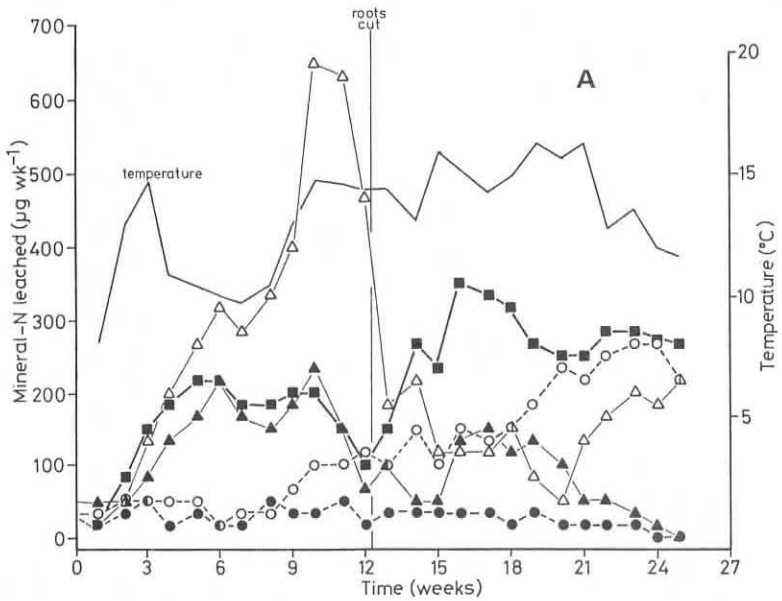

FIG. 1 A

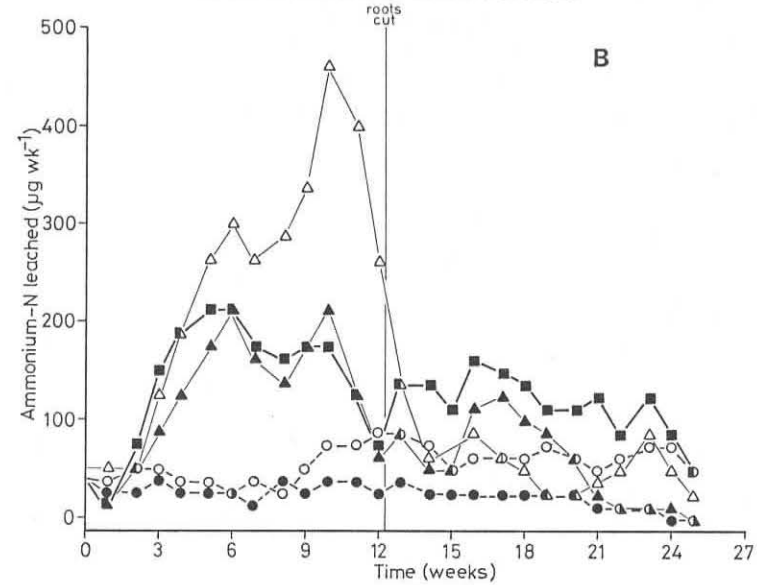

FIG. 1 B

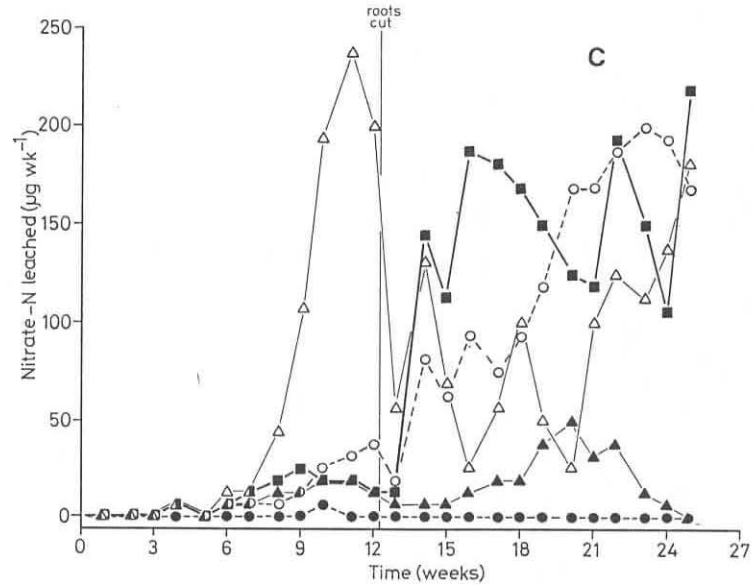

FIG. 1 C

FIG. 1. — Total mineral-N (A), ammonium-N (B) and nitrate-N (C) losses from oak leaf litter in field chambers with and without millipedes (added on week 1) and with or without living tree roots. Values shown are mean mineral-N losses in µg/chamber/week. Note that the scales for mineral-N are different in the three figures. The treatments are indicated as follows: without roots (open symbols) with (Δ) or without (○) animals; with roots (solid symbols), with (▲) or without (●) animals, and with animals where the roots were cut in week 12 (■). Integrated mean soil temperatures for the site are shown in (A).

C) Mineral-N fluxes during weeks 1-12

Several chambers were damaged by cattle escaping into the woodland during the first 2 months of the experiment and in addition, possibly as a consequence of disturbance, the roots subsequently died in five chambers. No damage or root death had occurred in previous experiments so additional replicates had not been included in the experimental design. The remaining chambers were therefore regrouped and, in order to maintain replication, the planned treatment of cutting roots linked to treatments without animals was abandoned.

The time-course of total mineral-N and nitrate-N losses from the chambers is shown in Figure 1.

Total mineral-N losses from the controls ($-A-R$) increased slowly over the first 3 months and contained a relatively constant component of ammonium-N while nitrification increased with time.

The effects of adding animals ($+A-R$) were evident from week 2 onwards and ammonium-N losses increased to a maximum in week 10, to about 6 times control levels, and then declined rapidly in weeks 12 and 13. Nitrate losses in these treatments showed a lag of about 6 weeks after enhanced ammonium release before increasing rapidly to a maximum in week 11.

Low nitrate concentrations were recorded in leachates from systems without animals ($-A+R$) but while ammonium-N losses were enhanced in the animal treatments with roots ($+A+R$ and $+A+R_c$), nitrate-N losses remained low.

Cumulative mineral-N losses from all treatments are shown in Table I and results of two-way ANOVA analyses in Table II. The results show that treatments with animals and without roots ($+A-R$) lost 5 times more mineral-N than treatments without animals, but the proportion of nitrate-N is similar in both treatments at 18.2% without animals ($-A-R$) and 20.7% with animals ($+A-R$).

Total mineral-N losses from root treatments, with and without animals, are about half those from treatments without roots. Although the animals maintained higher ammonium concentrations in rooted treatments the proportions of nitrate-N in rooted treatments with and without animals were again closely similar (4.5% in $-A+R$ and 4.6% in $+A+R$). However, the proportion of nitrate in total mineral-N in leachates was significantly ($P < 0.01$) lower in the presence of roots (0.16, 0.20 $-R$; 0.05, 0.06 $+R$; Tab. I).

D) Mineral-N fluxes during weeks 13-35

The addition of a further increment to all treatments in week 12 had no identifiable effects on trends for total mineral-N fluxes (*Fig.* 1 A): no changes in the pattern of mineral-N losses from rooted treatments are evident, the trend of decreasing mineral-N losses from the animal treatment without roots ($+A-R$) was continued and microbial mineralization of N in the controls ($-A-R$) continued to increase.

The effects of cutting the roots in treatment $+A+R_c$ resulted in nitrate-N losses increasing eleven times from 13.3 ± 2.7 µg N in week 13 to 151.1 ± 52.0 µg N in week 14 (*Fig.* 1 C). Thereafter nitrate-N losses remained high and variable. Total mineral-N losses from the controls ($-A-R$) continued to increase but nitrification

TAB. I. — **Cumulative mineral-N and hydrogen ion losses in leachates from leaf-litter in experimental chambers with and without implanted tree roots, and with and without millipedes. Animals were added after a five-week establishment period in the field and the leachates were monitored for 12 weeks. Roots linked into two animal treatments (animals/roots$_c$) were then cut and leachates monitored for a further 12 weeks in all treatments. Mean values (µg/unit) are shown with cumulative totals for two replicates per treatment in parentheses.**

WEEKS 1-12					
Treatment	Control	Animals only	Roots only	Animals/roots	Animals/roots$_c$
NH_4-N	**617.2** (547,5, 686.9)	**2,937.6** (2,764, 3,111)	**354.0** (419,4, 276.7)	**1,532.9** (1,661, 1,405)	**1,789.1** (1,656, 1,919)
NO_3-N	**151.3** (56.8, 245.7)	**559.0** (585.1, 532.9)	**23.2** (22.5, 11.9)	**82.6** (122.2, 43.0)	**131.4** (79.2, 183.6)
Total-N	**768.5** (604.3, 932.6)	**3,496.5** (3,349, 3,644)	**377.2** (441.9, 288.6)	**1,615.5** (1,784, 1,448)	**1,914.0** (1,724, 2,103)
Hydrogen	**1.34** (1.30, 1.37)	**0.82** (0.97, 0.66)	**1.66** (1.52, 1.79)	**1.66** (2.22, 1.10)	**1.39** (1.60, 1.17)
NO_3-N/Total-N	**0.20**	**0.16**	**0.06**	**0.05**	**0.07**
WEEKS 13-24					
Treatment	Control	Animals only	Roots only	Roots/animals	Animals/roots$_c$
NH_4-N	**885.8** (834.3, 937.2)	**876.8** (900.9, 852.7)	**243.4** (329.6, 157.2)	**748.6** (774.7, 722.5)	**1,526.6** (2,238, 815.0)
NO_3-N	**1,581.8** (1,182, 1,982)	**1,155.2** (1,127, 1,184)	**20.2** (27.1, 13.3)	**245.4** (451.1, 39.6)	**1,644.9** (1,330, 1,960)
Total-N	**2,467.6** (2,016, 2,919)	**2,032.0** (2,028, 2,036)	**263.6** (356.7, 170.5)	**1,093.0** (1,226, 762.1)	**3,271.5** (3,568, 2,775)
Hydrogen	**1.94** (1.62, 2.26)	**1.64** (1.93, 1.35)	**2.91** (2.03, 3.79)	**3.04** (3.79, 2.29)	**2.19** (1.32, 3.05)
NO_3-N/Total-N	**0.64**	**0.57**	**0.08**	**0.22**	**0.50**

TAB. II. — **Variance ratios (F) for two-way ANOVA on mineral-N and hydrogen ion losses in leachates from leaf litter presented in Table I.**

WEEKS 1-12						
Source	d. f.	Ammonium	Nitrate	Total-N	Hydrogen	NO_3-N/Total-N
Animals	1	217.4***	20.0*	19.1*	0.09	0.08
Roots	1	46.6**	33.3**	63.1**	3.79	11.34**
Interaction	1	22.8**	10.5*	191.3***	0.77	0.04
WEEKS 13-24						
Source	d. f.	Ammonium	Nitrate	Total-N	Hydrogen	NO_3-N/Total-N
Animals	1	21.7**	0.2	0.33	0.02	0.17
Roots	1	52.4**	30.0**	39.4**	3.69	13.0*
Interaction	1	23.3**	2.1	5.1	0.12	1.05

Significance ($F_{1,4}$): * $P < 0.05$, > 0.01; ** < 0.01, > 0.001; *** $P < 0.001$.

increased rapidly over the last 3 months of the experiment. All three of the treatments without roots ($-A-R$, $+A-R$ and $+A+R_c$) showed similar nitrate-N losses by week 25 compared with insignificant nitrate-N losses from rooted treatments ($+A+R$ and $-A+R$).

Cumulative mineral-N losses from treatments over weeks 13 to 25 are shown in Table I. The main features of these data are that total mineral-N losses from animal treatments and controls without roots ($-A-R$ and $+A-R$) are not significantly different, nitrate-N losses from the controls without roots ($-A-R$) are more than 70 times higher ($P < 0.001$) than losses from rooted treatments ($-A+R$), and cutting the roots increased nitrate losses by 12.5 times ($P < 0.001$) to levels similar to those in unrooted treatments.

The results of 3-way anova showed significant ($P < 0.001$) main effects of time for ammonium reflecting lower cumulative leachate concentrations for ammonium-N in animal and root treatments (animals/time, $P < 0.001$; root/time, $P < 0.01$) in the second half of the experiment (Tab. I). Main time effects were also significant ($P=0.001$) for nitrate with increased nitrate losses from animal treatments (animals/time, $P < 0.05$) but not for roots. As a consequence of these differences in directions of time-trends for nitrate and ammonium, main time effects for total-N were insignificant. Three-way interactions for animals/roots/time were significant for ammonium ($P < 0.001$) and total-N ($P=0.002$) but not for nitrate ($P=0.06$).

We discount denitrification as a source of variability in nitrate-N fluxes. Measurements of denitrification, in a similar series of experiments, using the acetylene inhibition assay (Yoshinari & Knowles, 1976), showed an extremely variable response in animal treatments with maximum rates of 10.0 ng N hr^{-1} g^{-1} litter at 15°C (Ineson & Anderson, unpublished data). If this rate was maintained for 7 days the cumulative nitrogen losses from the chambers would only amount to 3.5 μg N wk^{-1} and represent insignificant losses of nitrate-N in relation to the total fluxes.

E) Leachate pH

Leachate pH values ranged between 4.5 and 5.2 in all treatments during the course of the experiment. No major pH changes were associated with observed phases of enhanced ammonification or nitrification. Analysis of variance on cumulative H^+ concentrations in leachates for individual chambers (Tab. I) showed no significant differences between treatments (Tab. II).

III. – DISCUSSION

Autotrophic nitrifiers have characteristically slow growth rates; particularly under low pH conditions. The optimum pH range for both *Nitrosomonas* spp. and *Nitrobacter* spp. is pH 7 to 9 with inhibition below pH 6; though slow nitrification rates have been reported as low as pH 4.5 (Prosser & Cox, 1982). Therefore all the treatments in this series of experiments fall within a range of pH values where a delayed response by autotrophic nitrifiers to increased ammonium availability would be predicted.

The extended period of time (12 weeks) before the onset of nitrification in litter without animals ($-A-R$) is consistent with substrate limitations and pH constraints on the growth and activity of nitrifier populations. Under the same pH conditions, but with enhanced ammonium availability, rapid nitrification started 5 to 6 weeks earlier in animal treatments ($+A-R$). The onset of nitrification in week 6 or 7 occurred when ammonium-N losses were about 90 to 120 μg N g^{-1} wk^{-1} and close to the threshold of 60 to 90 μg N g^{-1} wk^{-1} above which Vitousek *et al.* (1982) found that nitrification usually occurred in forest floor materials incubated for 8 weeks in the laboratory.

Nitrifying bacteria have a poor capacity to competitively exploit ammonium (Jones & Richards, 1977) and the low nitrate concentrations in $-A+R$ treatments appears consistent with the hypothesis that an effective root sink for ammonium regulates nitrifier activity through substrate limitation (Verstraete, 1981; Cooper, 1986; Riha *et al.*, 1986). But the difference between mineral-N losses from animal treatments with and without roots (Tab. I) suggests that only half of the animal-mobilised N was taken up by the roots and concentrations of the remaining ammonium are above the threshold where extensive nitrification occurred in the animal treatments without roots. This could be taken as evidence that some additional factor regulating nitrification is associated with the presence of roots but is inconsistent with the allelopathy hypothesis given the response to cuttiing roots. Harmer & Alexander (1985) found long-term inhibition of nitrification in trenched plots in a spruce forest but were unable to account for the effect. Purchase (1974) has suggested that nitrification may be limited by phosphorus availability where roots scavenge P more effectively from the soil than nitrifiers. We have no information on P availability in these experiments but this interpretation seems unlikely since P uptake by mycorrhizas is often investigated in excized roots and fine roots can persist in a living state for months in the soil after connection with the parent tree has been severed (Ferrier & Alexander, 1985). Hence cutting the roots in these experiments would not have an immediate effect on P availability. Furthermore, the rapidity and magnitude of the nitrate losses following root cutting is inconsistent with the low specific growth rates for nitrifying bacteria under sub-optimuum conditions such as low pH environments (Prosser & Cox, 1982).

Our interpretation of the lower proportion of nitrate in leachates from rooted treatments (Tab. I) supports the contention of Vitousek & Reiners (1975) that high ratios of ammonium-N to nitrate-N in forest soils may reflect preferential uptake of nitrate and not inhibition of ammonium oxidation. This is also reflected by the results of another series of root implant experiments at the Perridge site (Anderson *et al.*, 1985 *a*) in which leaf litter releasing mineral-N as ammonium was replaced with nitrifying humus material from another site. The same undisturbed root/mycorrhizal system was immediately effective in absorbing nitrate and negligible nitrate concentrations were found in leachates, as in the present experiments. Rygiewicz *et al.* (1985 *a*, *b*) have shown that mycorrhizas which are normally taking up nitrogen as ammonium are also effective sinks for nitrate. We therefore predict that the onset of nitrification in the treatment with roots and animals was similar to that in the animal treatments without roots but nitrate produced in response to the enhanced N mineralisation by millipedes was taken up efficiently by the roots. We also predict that treatments with roots but no animals would not have shown rapid nitrate losses when the roots were cut in week 12 because of substrate limitation for nitrifiers; unfortunately this series of treatments was lost.

In conclusion, we have shown that the presence of roots and/or macrofauna have major effects on the onset and magnitude of ammonification and nitrification in litter. During the first 12 weeks of the experiment 11.4% of the total litter-N pool (30.5 mg) was lost from the animal treatments in the absence of a root sink compared with 2.5% attributable to microbial processes alone. Thereafter microbial N-mineralization increased as animal effects declined. This transient effect of animals, on what appears to be a discrete pool of readily-available organic-N (ANDERSON & INESON, 1984), therefore represents only a small proportion of the total-N in litter ultimately mobilized by microorganisms. But the timing of the animals effects, including patches of enhanced nitrification, might be significant in relation to seasonal patterns of litterfall and root uptake of nitrogen and other elements.

The mechanisms controlling nitrification and the significant animal/root interactions in these experiments have not been fully resolved but the approach offers considerable potential for more specific manipulative studies on animal, microbial, mycorrhizal and root components of the system.

ACKNOWLEDGEMENTS

We are grateful to Mark MACNAIR and David KNIGHT for assistance with statistical analysis and to Ian ALEXANDER for helpful comments on the manuscript.

SUMMARY

Small experimental chambers containing oak leaf litter were established in an oak woodland with and without millipedes, and with and without tree root implants to act as mineral-N sinks. The systems were monitored for 25 weeks in the field between April and October. The animals altered the timing of N mineralisation by enhancing ammonification during the first 3 months of the experiment while microbial mineralisation processes alone increased in the second 3 month period. There was a time lag of several weeks before the onset of nitrification but in the animal treatments (without roots), with enhanced ammonium concentrations, nitrification started 6 weeks earlier than in controls without animals. Negligible nitrate losses occurred from treatments with animals and roots although high ammonium concentrations were present. When the roots were cut in one series of animal treatments nitrate losses increased 11 times within 7 days. It is concluded that low ammonium availability and low pH account for the time lag and/or low rates of nitrification in treatments without animals and with and without roots. But the efficient uptake of nitrate by roots may account for the apparent inhibition of nitrification in treatments with animals.

RÉSUMÉ

Effets des racines de chêne et de la macrofaune sur la nitrification et les pertes en azote dans une litière de forêt décidue

De petits modules expérimentaux contenant des fragments de feuilles de chêne ont été mis en place dans une forêt de chêne avec et sans diplopodes. Dans une partie d'entre eux on a introduit des racines pour immobiliser l'azote minéral. Ces différents systèmes ont été contrôlés chaque semaine pendant 25 semaines entre avril et octobre. Les animaux ont modifié la cinétique de la déminéralisation de l'azote en augmentant l'ammonification pendant les trois premiers mois de l'expérience alors que le processus de minéralisation microbienne augmentait durant la deuxième période de 3 mois. On observe un délai de plusieurs semaines avant le commencement de la nitrification mais, dans l'expérience avec diplopodes et sans racines, et avec des concentrations augmentées en ammonium, la nitrification a commencé 6 semaines plus tôt que dans les témoins sans animaux. Des pertes négligeables de nitrate apparurent dans les systèmes avec racines et avec animaux, bien que de fortes concentrations en ammonium soient permanentes. Les systèmes avec animaux dont les racines ont été coupées présentèrent une perte en nitrate multipliée par 11 en 7 jours. En conclusion, la faible disponibilité d'ammonium et le faible pH seraient responsables du décalage dans le temps et/ou du faible taux de nitrification dans les expériences sans animaux, avec ou sans racines. L'assimilation efficace de nitrate par les racines peut expliquer l'inhibition apparente de la nitrification dans l'expérience avec racines et sans animaux.

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